REVISTA IBÉRICA de Aracnología

ARTÍCULO:

Four additional specimens of the fossil camel spider *Cratosolpuga wunderlichi* Selden 1996 (Arachnida: Solifugae) from the lower Cretaceous Crato formation of Brazil

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Revista Ibérica de Aracnología
ISSN: 1576 - 9518.
Dep. Legal: Z-2656-2000.
Vol. **9**, 30-VI-2004
Sección: Artículos y Notas.
Pp: 143–156.

Edita: **Grupo Ibérico de Aracnología (GIA)**
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FOUR ADDITIONAL SPECIMENS OF THE FOSSIL CAMEL SPIDER *CRATOSOLPUGA WUNDERLICHI* SELDEN 1996 (ARACHNIDA: SOLIFUGAE) FROM THE LOWER CRETACEOUS CRATO FORMATION OF BRAZIL

Jason A. Dunlop & David M. Martill

Abstract:

Four new camel spider specimens (Arachnida: Solifugae) in the Berlin and Stuttgart collections are described from Lower Cretaceous (Aptian) strata of the Crato Formation, Ceará, Brazil. The new material can be referred to the ceromid solifuge *Cratosolpuga wunderlichi* Selden 1996, and displays morphological details not seen in the type specimen. These include cheliceral dentition, tactile hairs, the dorsal surface and ornament of the opisthosoma and an extensive membrane between the tergites and sternites. All confirm the essential modernity of the Crato material and one specimen is preserved as an unusual lateral compression. Camel spiders are characteristic of desert regions and support the hypothesis that the Crato Formation lagoon was at times surrounded by an arid hinterland.

Key words: Arthropoda, Arachnida, Solifugae, Paleontology, Cretaceous, Brazil.

Cuatro especímenes adicionales del solífugo fósil *Cratosolpuga wunderlichi* Selden 1996 (Arachnida: Solifugae) del Cretácico linferior de la formación Crato en Brasil

Resumen:

Se describen cuatro nuevos especímenes de solífugos (Arachnida: Solifugae), depositados en las colecciones de Berlín y de Stuttgart, que proceden de estratos del Cretácico Inferior (Aptiano) de la formación Crato, Ceará, Brasil. El nuevo material se puede referir al cerómido *Cratosolpuga wunderlichi* Selden 1996 y exhibe detalles morfológicos no considerados en el material tipo. Éstos incluyen la dentición queliceral, los pelos táctiles, la superficie y el ornamento dorsal del opistosoma y una membrana extensa entre los terguitos y los esternitos. Todos confirman la modernidad esencial del material de Crato y un espécimen se preserva como compresión lateral inusual. Los solífugos son característicos de regiones desérticas y apoyan la hipótesis de que la laguna de la formación Crato estuvo rodeada ocasionalmente por un ambiente árido.

Palabras clave: Arthropoda, Arachnida, Solifugae, Paleontología, Cretácico, Brasil.

Introduction

Mesozoic fossil arachnids are generally very rare. Well preserved material from the Lower Cretaceous Crato Formation of Ceará State, Brazil is therefore important for our understanding of arachnid palaeodiversity and evolution. These Crato arachnids generally look very modern and can often be assigned to extant families (see below). The Crato Formation arachnofauna includes spiders (Araneae), scorpions (Scorpiones), whipspiders (Amblypygi), whipscorpions (Uropygi) and camel spiders (Solifugae); see e.g. Dunlop & Martill (2002) for further literature. Tiny fossil eggs attached to bird feathers have also been described (Martill & Davis, 1998, 2001) and could be evidence for mites (Acari).

Camel spiders (also called sun spiders, wind scorpions or solifuges) are among the rarest fossil arachnids. A possible stem-group form was described from the Lower Carboniferous of Poland (Dunlop & Rößler, 2003), while the oldest unequivocal camel spider – still only barely recognisable as a member of the order – comes from the Upper Carboniferous Coal Measures of Illinois, USA (redescribed by Selden & Shear 1996). There are two Tertiary records of solifuges: an ammotrechid from Dominican amber (Poinar & Santiago-Blay, 1989) and a daesiid from Baltic amber (Dunlop *et al*. in press). Mesozoic camel spiders are known only from the Nova Olinda Member of the Crato Formation. A mature male and a conspecific smaller juvenile were described in detail by Selden & Shear (1996). *Cratosolpuga wunderlichi* Selden 1996 was assigned to the extant, southern African family Ceromidae. These authors also discussed the biogeographical implications of this assignment, namely that ceromids were originally more widespread on the palaeocontinent of Gondwana, but subsequently died out in South America. Here we describe four new well-preserved Crato Formation camel spiders held in the Berlin and Stuttgart collections.

Materials and methods

The fossils described here are held in the arthropod palaeontological collections of the Museum für Naturkunde, Berlin, Germany (MB.A. numbers 1087 and 1088) and the Staatliches Museum für Naturkunde in Stuttgart, Germany (SMNS 65417 and 65418). The Berlin specimens were prepared using a dissecting needle to gently remove pieces of the relatively soft matrix obscuring details of the body. The Stuttgart fossils had been prepared previously. The specimens were drawn using a *camera lucida* and compared to extant solifuges in the zoological collections of the Museum für Naturkunde; in particular the ceromid *Ceroma ornatum* Karsch 1885. Morphological terminology, including the identity of leg podomeres, mostly follows Selden & Shear (1996).

Geological setting

The geological setting and associated biota of the Crato arachnid fossils has been reviewed by, e.g. Martill (1993), Selden & Shear (1996) and Dunlop & Martill (2002). In overview, the fossil-bearing Nova Olinda Member of the Crato Formation of southern Ceará, northeast Brazil is a finely laminated limestone Konservat-Lagerstätte dated, on palynological evidence (Pons *et al*., 1990), as Aptian (Early Cretaceous; ca. 115 Ma). The Crato Formation has become famous for its abundant, diverse and very well preserved flora and fauna which occurs in the lowest 3-15 metres of the unit. This part of the sequence comprises an uninterrupted sequence of millimetrically laminated carbonates known as the Nova Olinda Member (Martill 1993). It is particularly well-known for insects – see e.g. Schlüter (2003) for a review and additional literature – and for vertebrate fossils (e.g. Martill 1993); the latter including fish, pterosaurs and other tetrapods. The insect and arachnid fossils are typically preserved as reddish-brown geothitic pseudomorphs on a pale yellow limestone matrix in the weathered stone or as black, pyritic carbonised replicas on a dark blue/grey matrix in the fresh stone. Voids within the fossils are usually filled with clear calcite. Preservation is often excellent and slightly three-dimensional and many fossils include fine details such as the hairs or pores found in the cuticle of the type specimen of *C. wunderlichi* (Selden & Shear, 1996; see also below).

Abbreviations

The following abbreviations are used as standard in the illustrations: bs basifemur (or femur 1); cb cylinder bristles of pedipalp; ch chelicera; cl tarsal claws; cx coxa, dn dentition of cheliceral fingers; fe femur; el external lobe of propeltidium; ey eye tubercle; fi fixed finger of chelicera; fr free finger of chelicera; gs genital sternite; mb membrane between tergites and sternites; me median plagula; ms median sulcus of propeltidium; mt metapeltidium; pl pedipalp; pr propeltidium; pt patella; st spine-like setae; te telofemur (or femur 2); th tactile hair; ti tibia; tr trochanter; ts tarsus; legs numbered from 1–4.

Morphological interpretation

Camel spider morphology has been summarised by Punzo (1998) and, as noted by Selden & Shear (1996), the Crato fossils (Figs. 1-8) are essentially modern-looking forms which can be assigned to a living family.

Prosoma

The camel spider carapace is divided into a number of discrete sclerites, the largest of which is the propeltidium (Figs. 5, 7). This is a vaulted, usually semicircular structure bearing the median eyes on a slightly raised tubercle (Figs. 6, 8). As in these fossils, in certain extant taxa the anterolateral corners of the propeltidium form small external lobes (Figs. 1, 3) that are to some degree separated from the rest of the propeltidium. Immediately behind the propeltidium – and incorporated with it as part of the same tagmata – is the parapeltidium forming a sclerotised band called the median plagula (Figs. 5, 7). This complex is followed by two more somites associated with legs 3 and 4. They are represented by small sclerites termed the meso- and metapeltidium respectively. Ventrally (Figs. 2, 4) the pedipalp and limb coxae form the floor of the prosoma. There is no sternum between them. The coxae of the middle legs in particular (2 and 3) are somewhat quadrate. The coxae and other proximal podomeres of the last pair of legs usually bear enigmatic sensory organs called malleoli or racquet organs, but these have yet to be seen in the Crato material.

Chelicerae/pedipalps

Camel spiders are characterised by massive, chelate chelicerae in which a ventral free finger articulates against a dorsal fixed finger. These cheliceral fingers are typically dentate (Figs. 6, 8) and setose (Figs. 1, 3). One specimen, MB.A. 1088, includes setal sockets on the ventral surface of the fixed finger. The pedipalps are robust, thicker than the legs, and beyond the trochanter consist of three relatively long podomeres (femur, patella, tibia), plus a short tarsus (Figs. 2, 4) that in living taxa ends in a sucker-like organ. As in the fossils (Figs. 1, 3, 5, 7), camel spider pedipalps often bear a row of stout, blunt, inwardly-facing, spine-like setae which some authors (e.g. Wharton 1981) term cylinder bristles and which may play a role in prey capture.

Legs

Camel spider leg podomeres and their homology with other arachnids have proven controversial (see Selden & Shear, 1996, table 1). Studies of musculature suggest that the largest leg podomere – which resembles the femur of other arachnids – is in fact the patella (Figs. 2, 4) and that the third and fourth pair of legs retain a basi- and telofemur; alternatively named femur 1 and femur 2. The first leg pair is usually more gracile than the others and with the exception of some fossorial taxa, the legs tend to be quite long. Indeed camel spiders are noted in the literature for their speed. The tarsi at the ends of the legs can be subdivided into tarsomeres and the distal ends of the legs in particular often bear stout spines (Figs. 1, 3). Both tarsomere number and spines are of taxonomic significance in living solifuges. The legs in particular also usually bear long sensory setae known as tactile hairs. These can be very long and MB.A. 1087 (Figs. 1, 3) shows the first evidence for long tactile hairs in Crato camel spiders. At least the third and fourth pair of tarsi in this specimen end in a pair of large, curving claws (Figs. 1, 3). Among extant taxa leg 1 often lacks claws and the animals are effectively hexapodal, running on legs 2-4 and using leg 1 as a more tactile appendage.

Opisthosoma

The camel spider opisthosoma consists of ten segments, although none of the Crato fossils preserve the opisthosoma in its entirety. Dorsal tergites and ventral sternites are separated by a flexible, expandable membrane, clearly preserved here in both MB.A. 1087 (Figs. 1, 3) and SMNS 65418 (Figs. 6, 8). Dorsally MB.A. 1087 reveals for the first time in the Crato fossils the dorsal opisthosoma with its raised ridge of tubercles along the midline of the tergites and a degree of rebordering of the tergites along their lateral and posterior margins. Posteriorly they become increasingly recurved. This raised median ridge on the tergites is seen in some living camel spiders and can even be discerned in a possible stem-line form from the Carboniferous (Dunlop & Rößler 2003). Ventrally, the genital sternite (Figs. 2, 4) in MB.A. 1088 appears to be bilobed, with evidence for an ill-defined medial division. This feature is also seen in, for example, some extant ceromid camel spiders (pers. obs. on *C. ornatum*) and reinforces the hypothesis that the Crato fossils are essentially modern-looking creatures.

Order SOLIFUGAE Sundevall 1833

Family Ceromidae Roewer 1934

Genus *Cratosolpuga* Selden 1996 (in Selden & Shear)

Cratosolpuga Selden, in Selden & Shear 1996: p. 601. Harvey, 2003: p. 212.

Diagnosis (After Selden in Selden & Shear, 1996): Male cheliceral flagellum attached to dorsomedial side of chelicera near base of fixed finger, consisting of globose base and styliform whip extending directly backwards to base of chelicera, stiff membrane partly enclosing flagellum base and running length of flagellum forming a narrow gutter. Single tarsomere on all legs.

Cratosolpuga wunderlichi Selden 1996 (in Selden & Shear)

Figs. 1-8.

Cratosolpuga wunderlichi Selden, in Selden & Shear 1996: pp. 584, 588-595, 601-603, pl. 1, figs. 2-4, pl. 2, text-figs. 1, 3-6 A-G. – Punzo 1998: pp. 213-214, figs. 7.7-7.10. – Dunlop & Martill 2002: p. 325. – Harvey 2002: p. 366. - Harvey 2003: p. 212.

Cratosolpuga [*wunderlichi*]: Dunlop 1996: pp. 84, 86, fig. 5.

Material: MB.A. 1087 and 1088. SMNS 65417 and 65418. All from the Nova Olinda Member, Crato Formation, southern Ceará, northeast Brazil. Early Cretaceous (Aptian).

Diagnosis: As for the genus.

Description (MBA 1087)

Measurements (in mm) – Total body length (including chelicerae) 20.3. Prosoma (without chelicerae) 4.9. Opisthosoma 9.7 long; maximum width 4.9. Four distinct opisthosomal tergites, lengths 1.2, 1.1., 1.1 and 0.9, widths 2.6. Cheliceral length 5.7. Pedipalp podomere lengths: femur 4.7, patella 5.4, tibia 4.7, tarsus 1.0 (total length 15.8). Leg 1 total length c. 15. Incomplete leg 2, total preserved length c. 9. Leg 3 total length c. 15. Leg 4 total length c. 22.

Medium-sized solifuge (Figs. 1, 2) in dorsal view. Preservation faint in places. Chelicerae preserved mostly in outline, with brushes of setae on both the mesal and lateral sides of the fixed finger. Propeltidium preserved mostly in outline. Median eye tubercle prominent and external lobes present. Elements of meso and metapeltidium also preserved, but sclerite boundaries indistinct. Limbs on right side particularly well preserved, those on left side incomplete. Pedipalps robust with strong, infacing cylinder bristles on femur, patella and tibia. Leg 1 gracile, legs 2-4 more robust, all with short, spine-like setae on the more distal podomeres. Precise podomere boundaries hard to define and number of tarsomeres (i.e. subdivisions of the tarsus) equivocal. Leg 3 with at least one long and one short tactile hair. Legs 3 and 4 with slender tarsal claws. Leg 4 noticeably longer than other limbs.

Opisthosoma oval, widest about two thirds of the way along its length. Four subrectangular tergites clearly preserved, increasingly recurved posteriorly, rebordered along lateral and posterior margins and all with raised midline region becoming more diffuse posteriorly. Three tergites show slight subdivision or lineation in the posterolateral regions. More posterior tergites mostly missing, but some indication of shorter tergites at posterior end of opisthosoma. Tergites bordered laterally by distinct, folded membrane extending the length of the opisthosoma, but clearly separated into regions corresponding to the adjacent tergites.

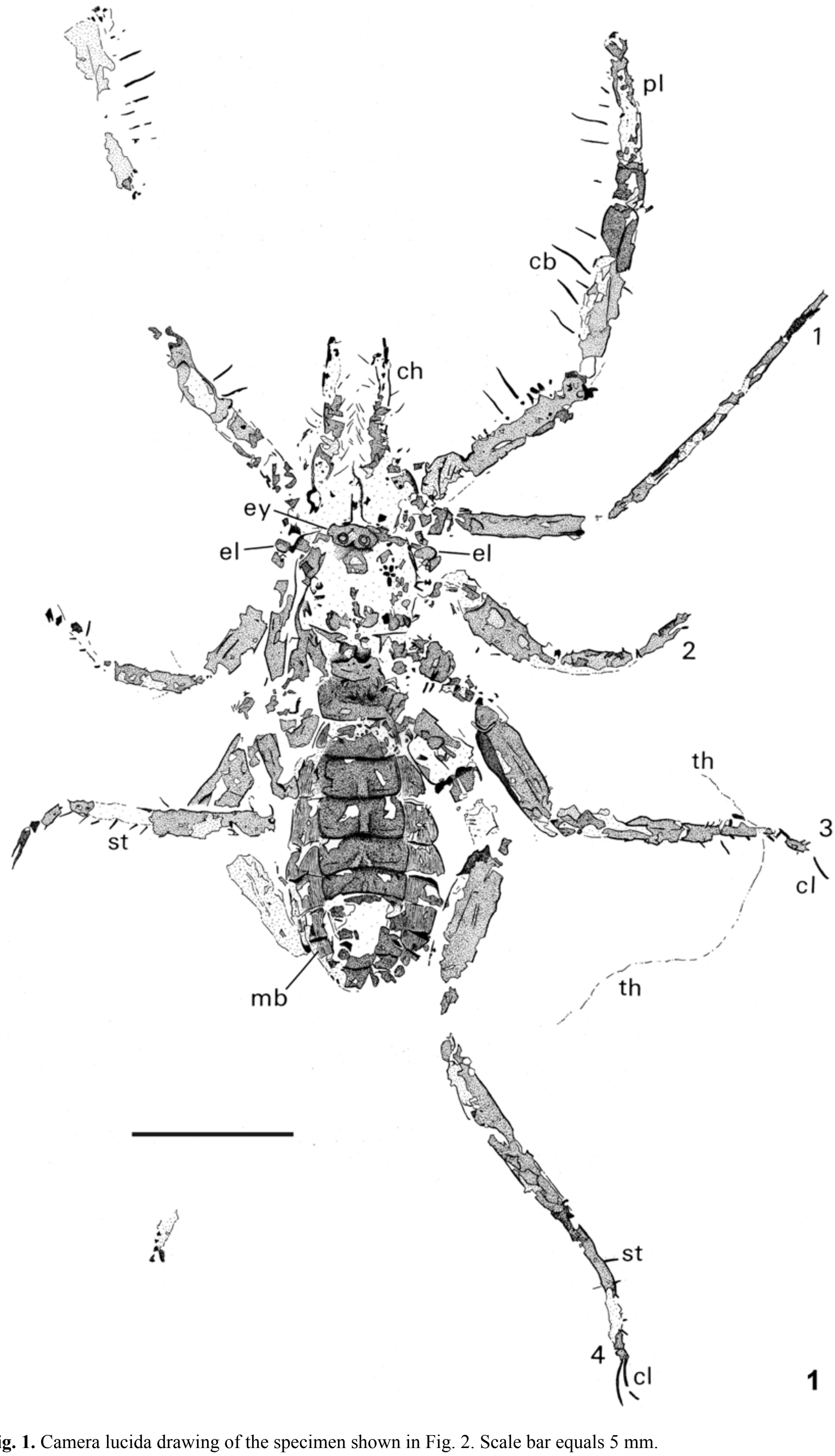

Fig. 1. Camera lucida drawing of the specimen shown in Fig. 2. Scale bar equals 5 mm.
Fig. 2. *Cratosolpuga wunderlichi* Selden 1996. MB.A. 1087, from the Nova Olinda Member, Crato Formation, southern Ceará, northeast Brazil. Early Cretaceous (Aptian). '

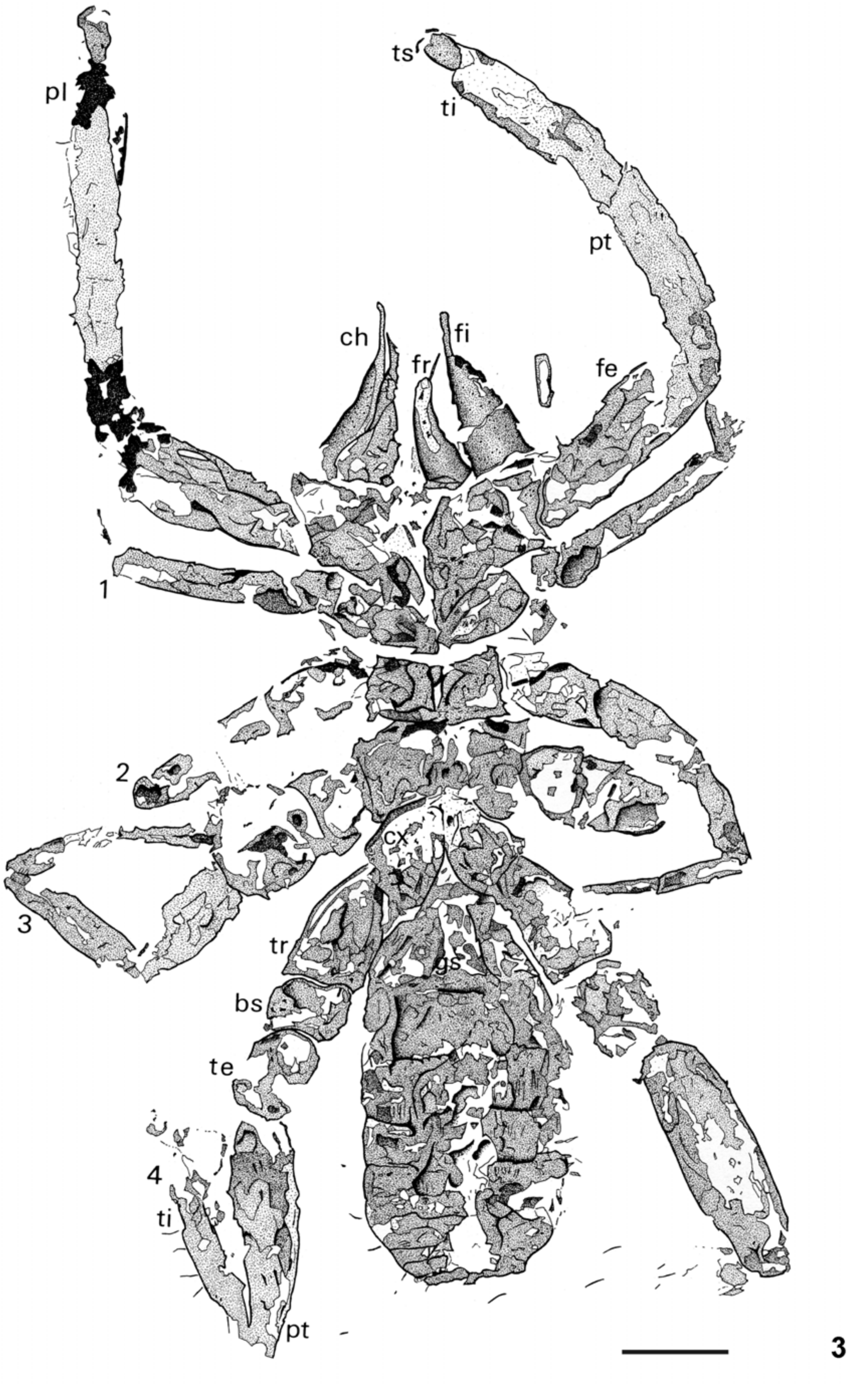

Fig. 3. Camera lucida drawing of the specimen shown in Fig. 4. Scale bar equals 2 mm.
Fig. 4. *Cratosolpuga wunderlichi* Selden 1996. MB.A. 1088, from the Nova Olinda Member, Crato Formation, southern Ceará, northeast Brazil. Early Cretaceous (Aptian). '

Description (MB.A. 1088)
Measurements (in mm) – Total body length (including chelicerae) 14.4. Prosoma (without chelicerae) 5.1. Cheliceral length 2.7. Pedipalp podomere lengths: femur 3.0, patella 2.8, tibia 3.0, tarsus 0.7 (total length 9.5). Leg 1 patella 2.0. Leg 2 podomere lengths: femur 0.92, patella 1.7, tibia 1.7, basitarsus 1.2, telotarsus 1.1. Leg 3 podomere lengths: patella 1.8, tibia 2.4, basitarsus 1.7, telotarsus 1.4. Leg 4 podomere lengths: trochanter 1.6, basifemur 0.76, telofemur 1.4, patella 3.5. Opisthosoma 6.6 long; maximum width 3.0.

Small, probably juvenile solifuge in ventral view (Figs. 3, 4). Cuticle dark brown against the matrix. Chelicerae, pedipalps and coxal region well preserved, distal ends of legs 1 and 4 less so. Chelicerae characteristically massive. Fixed finger with distinct setal sockets on ventral surface. Further setal sockets preserved on proximal podomeres of pedipalps and leg 1. Pedipalpal coxae massive, subtriangular. Pedipalps robust. Leg 1 slender; incomplete. Coxae of legs 2 and 3 subquadrate. Legs 2 and 3 robust, mostly complete. Leg 4 coxae subtriangular. Proximal appendages clearly preserved with distally widening trochanter, short, quadrate basifemur and telofemur and longer, stout patella. More distal podomeres incomplete. Opisthosoma lozenge shaped with evidence for at least nine sternites. Sternites longer anteriorly, but becoming distinctly shorter posteriorly. Genital sternite large, subtriangular and apparently bilobed. Central part of posterior sternites badly distorted and broken up.

Description (SMNS 65417)
Measurements (in mm) – Total body length (including chelicerae) 14.7. Propeltidium length 2.3, maximum width 3.9. Cheliceral length 4.9. Six preserved opisthosomal tergites with lengths of 1.1, 1.0, 1.0, 0.8, 0.8 and 0.8. Preserved leg lengths: leg 1 c. 10, leg 2 c. 8, leg 3 c. 11.

Fairly small camel spider in dorsal view (Figs. 5, 6). Propeltidium semicircular; exterior lobes not preserved, but gaps in the anterolateral corners suggest their presence in life. Median eye tubercle present on anterior propeltidium border. Propeltidium divided by distinct medial suture. Pattern of four setal sockets around the suture; anterior pair more widely spaced than posterior pair. Elements of median plagula and (?)metapeltidium preserved behind the propeltidium. Chelicerae robust, but details lacking. Pedipalps large with cylinder bristles. Legs generally faint and in places only preserved in outline. Legs 1–3 relatively complete, but with indistinct podomere boundaries. Leg 4 incomplete, distal podomeres missing. Opisthosoma incomplete, especially laterally. Eight tergites preserved, six showing their full length. Tergites faint, but partly with darker patches of mineralisation.

Description (SMNS 65418)
Measurements (in mm) – Total body length (including chelicerae) 23.1. Cheliceral length 5.6. Preserved pedipalp length 24.1. Preserved leg 1 length 14.6. Preserved leg 4 length 29.7. Opisthosomal length c. 11, maximum thickness 3.4. Preserved opisthosomal segments vary in length between 1.5 and 0.7.

Large solifuge in lateral view (Figs. 7, 8). Cuticle particularly dark against the matrix. Propeltidium mostly indistinct, but median eye tubercle prominent and high. Chelicera robust, showing – partly in outline only – tapering fixed and free fingers. Free finger with dentition of at least two blunt teeth, a larger one proximally and a smaller one distally, while distal end of free finger appears to curve upwards at the tip. Chelicera also preserves a few associated setae. Lateral prosomal region hints at proximal-most podomeres of palps and legs, but preservation patchy and poor. Pedipalp robust. Anterior surface clothed with numerous fine setae. Leg 1 gracile and distally preserved mostly in outline only. Legs 2 and 3 larger, but proximal regions only preserved to loci where they cross leg 4. Fourth leg largest and longest. Both left and right legs preserved, with massive patella of right leg overlying left leg slightly. Leg 4 with a number of fine setae along its length. No evidence for tarsal division. Tarsal claws not preserved.

Opisthosoma rectangular in lateral view and bluntly tapering posteriorly. Tergites not clearly preserved and whole tergal region generally pale. Sternites better preserved, at least six discernible, generally becoming shorter posteriorly. Membrane between tergites and sternites very well preserved and defining at least eight opisthosomal segments. Membrane preserved as tightly packed longitudinal lines running along the opisthosoma. Most membrane areas clearly defined as opisthosomal segments, widest anteriorly and tapering posteriorly. Anterior margins of all membrane segments demarcated from the rest of the membrane; demarcated area becomes narrower going posteriorly.

Remarks: All four fossil solifuges newly described here differ slightly in both shape and preservation from the holotype of *Cratosolpuga wunderlichi.* It is tempting to recognise new taxa from among this material. However the taxonomic characters used in living solifuges (see e.g. Muma, 1951; Muma & Brookhart, 1988; Simonetta & Delle Cave, 1968; Wharton, 1981) predominantly relate to tarsal spination and tarsomere number, shape of the genital opercula, cheliceral shape and dentition, and the shape of the (male) cheliceral flagellum. With the exception of the tarsal podomeres and the flagellum in the *C. wunderlichi* holotype, all these features are somewhat equivocal in the Crato material and different fossils preserve different combinations of potentially diagnostic features. Overall size is invariably an unreliable character given the possibility of juvenile instars and Junqua (1966) suggested that adult size in Recent camel spiders may not be fixed. Muma & Brookhart (1988, p. 2) cautioned that among living taxa the size of the opisthosoma can be so variable that they regarded opisthosomal measurements as taxonomically irrelevant.

In MB.A. 1087 the absence of the dorsal cheliceral surface (and any flagellum) makes it difficult to sex this fossil. However, the overall shape and limb proportions appear to match the holotype quite closely. We see no evidence for more than one tarsomere (c.f. Selden's original diagnosis), thus we are confident about the referral of this specimen to *C. wunderlichi*. Specimen MB.A. 1088 is smaller and appears somewhat more robust than the holotype, as is the smaller specimen figured by Selden & Shear (1996, text-fig. 3) and presumed by these authors to be a conspecific juvenile. Detailed morphometric studies of ontogeny in living solifuges are lacking (c.f. Junqua 1966), but slight changes in proportions are perhaps to be expected. We see no explicit characters to justify a new taxon.

SMNS 65417 is also smaller than the *C. wunderlichi* holotype and does express one feature of interest, a distinct median suture on the propeltidium, which is not obvious in the holotype (Selden & Shear 1996, text-fig. 4). SMNS 65417 also lacks the raised medial tubercles on the opisthosoma in MB.A. 1087. However, a median suture has not been used as a taxonomic character in living solifuges and examination of intraspecific variation among Recent specimens (e.g. *C. ornatum*) in alcohol suggests that even within a species the degree to which a median suture is expressed can vary. The opisthosoma in this fossil looks quite small, but see the Muma & Brookhart comments above. Additional fossils may yet indicate two distinct morphologies – i.e. specimens with or without a divided propeltidium – but given the weakness of this one character among living camel spiders we are reluctant to raise a new taxon based on the material currently available. The final specimen, SMNS 65418 is unusual in that it is a lateral compression rather than the normal dorsal or ventral orientation. It again shows no evidence for multiple tarsomeres in the tarsus and thus fits the original diagnosis for *C. wunderlichi*. SMNS 65418 is the largest solifuge described thus far from the Crato Formation. Indeed body lengths range from c. 6 (Selden & Shear's juvenile) to c. 23 mm, strongly suggesting that multiple instars have been preserved.

Palaeoecology

Camel spiders are generally found in arid habitats (Punzo 1998). The presence of camel spiders in the Nova Olinda Member of the Crato Formation thus supports previous interpretations (Martill 1993) of a fairly arid hinterland environment surrounding a lake or lagoonal system where the biota has been preserved. Of interest is the presence in the Nova Olinda Member of wholly terrestrial organisms some distance from the palaeoshoreline. The Nova Olinda Member is a very pure limestone, with very little to no detrital sediment. While insects and pterosaurs may have flown over the lagoon, the terrestrial biota must have drifted into the basin from the margins, or via rivers entering the lagoon. A clue to the arrival mechanism of the camel spiders comes from the flora. Many plants occur in their entirety (Martill 1993) with the roots, stems and leaves attached. In one specimen a mass of soil remains attached to the roots. Thus it is likely that local rivers entering the Crato Formation lagoon were eroding their banks during floods. Plants and terrestrial fauna would have been undercut and washed into the lagoon as part of the flotsam and drifted toward the basin centre by wind currents, while the detrital sediment would have been deposited on the deltas.

Acknowledgements

We thank Christian Neumann (MB.A.) and Günter Bechly (SMNS) for the loan of material in their care and Antonio Melic and an anonymous reviewer for helpful comments on the text. Vera Heinrich (Berlin) prepared the photographs. DMM thanks Artur Andrade (D.N.P.M. Crato) and Paulo Brito for help with field work in Brazil. DMM was supported by NERC grant GR9/02503.

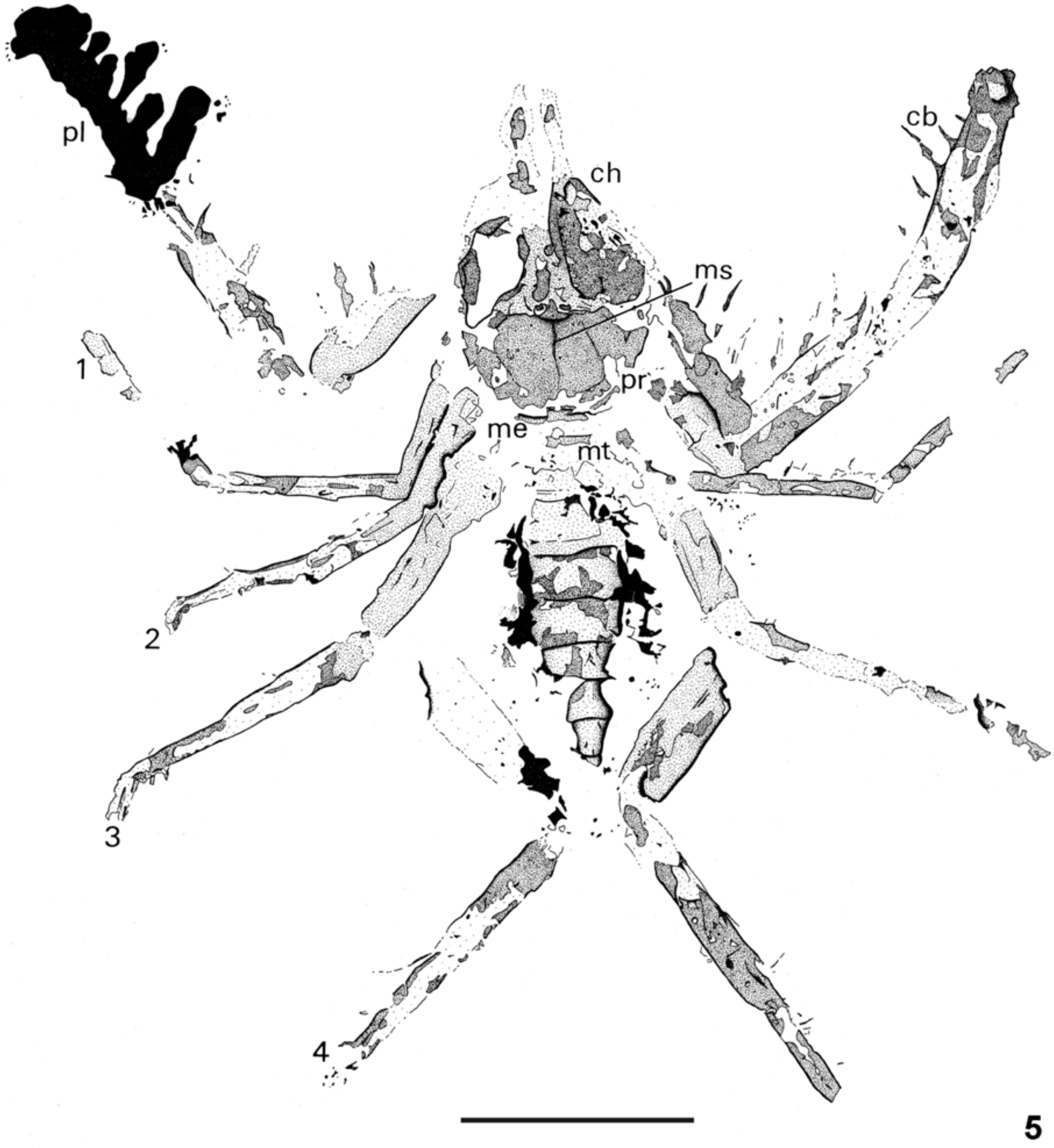

Fig. 5. *Camera lucida* drawing of the specimen shown in Fig. 6. Scale bar equals 5 mm.
Fig. 6. *C. wunderlichi* Selden 1996. SMNS 65417, from the Nova Olinda Member, Crato Formation, southern Ceará, northeast Brazil. Early Cretaceous (Aptian). '

Fig. 7. *Camera lucida* drawing of the specimen shown in Fig. 8. Scale bar equals 5 mm.
Fig. 8. *C. wunderlichi* Selden 1996. SMNS 65418, from the Nova Olinda Member, Crato Formation, southern Ceará, northeast Brazil. Early Cretaceous (Aptian).

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